

Observations on *Exaerete* spp. and their hosts *Eulaema terminata* and *Euplusia surinamensis* (Hymen., Apidae, Euglossinae) in Trinidad

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Abstract: In Trinidad the parasitic *Exaerete dentata* (Linn.) develops in the cells of *Euplusia surinamensis* (Linn.) and a second species in the cells of *Eulaema terminata* Smith. The female of *E. dentata* opens the recently sealed cell and removes the host's egg and after ovipositing reseals the cell. Females of *Exaerete* sp. were observed to enter a nest of *E. terminata* but activities within the nest could not be observed. In the discussion the behavior of *Exaerete* spp. is compared with other parasitic bees.

The appearance of the recent review on the evolution of parasitism among bees (Bohart, 1970) has prompted the preparation of the following notes on my somewhat limited observations on *Exaerete* spp. in Trinidad. In his review Bohart refers to the two parasitic Euglossine genera *Exaerete* and *Aglae* and states that little is known of the biology of these parasites, although he speculates that their habits are probably intermediate between those of *Psithyrus*, which invades nests of *Bombus* and after an initial struggle is accepted by the original queen and her workers, and those of most parasites of solitary bees in other families which surreptitiously insert their eggs in the partially provisioned or sealed cells when the host bees are absent.

Zucchi et al. (1969) in their comprehensive review of the biology of the Euglossinae also refer to the dearth of observations on the behavior of the parasitic members, although they cite most of the instances where definite host-parasite associations are known. In one other reference (Dodson and Frymire, 1961), *Exaerete smaragdina* Guer. is mentioned as a parasite of *Euplusia surinamensis* (Linn.) in Ecuador. Accordingly, the following observations may be of interest.

ASSOCIATION WITH *Eulaema terminata*

In Trinidad where three species of *Exaerete*, i.e., *dentata* (Linn.), *smaragdina* Guer., and an undescribed species near *frontalis* Guer. occur (J. G. Rozen, pers. comm., 1966; J. S. Moure, CMF, pers. comm., 1972), a female of this genus was observed on several occasions hovering near and entering a nest of *Eulaema terminata* Smith within a hollow tree.

The nest was discovered on April 9, 1964, by D. Bharath, who had earlier located another nest of this species (Bennett, 1965). While we were walking along a pathway in the Nariva Swamp he noted a female of *E. terminata*

enter a small opening in a tree trunk. The opening, oval-shaped, approx. 6 cm. \times 5.4 cm., situated 1.3 mm. from ground level, had been closed with mud except for a circular 1.5 cm. hole near the top. Arrangements were made for Mr. Bharath to make continual observations on activities near the entrance of the nest from early morning until late afternoon on April 15 and 16, and again from 10:30 A.M., April 21, until activity ceased on the afternoon of April 25.

(a) Activities of *E. terminata*: The pertinent observations are summarized in Table 1. When leaving the nest, females of *E. terminata* frequently disappear rapidly with little or no orientation flight, while returning bees usually hover momentarily before entering and hence the number of entries recorded for the day was usually greater than the number of departures, although on two occasions there were more observed departures than entries. It was discovered during the first day that returning females approached the nest entrance but retreated if the observer was close enough to attempt to determine whether nesting material or pollen was being carried. Accordingly, on only a few occasions was the nature of the load determined, although it was ascertained that either pollen or mud (nesting material) (never both) could be collected on the first morning trip. Frequently on an afternoon flight adults returned unladen and it is assumed that they had left the nest to collect nectar for their own use, a habit observed earlier in *Euglossa cordata* (author's unpubl. data). If laden in the afternoon, the load was invariably identified as pollen. Although the number of bees in the nest was not determined, an analysis of the departure and return times suggests that three or at most four females were active; for example, three females departed in rapid succession on the morning of April 16. There were two well-defined periods of flight activity, i.e., the first part of the morning and late afternoon. The time of first departure varied from 5:30 to 6:05 A.M., i.e., usually as the sky brightened in the east but before sunrise. The duration of the first afternoon flight varied from 25 minutes to almost two hours. The afternoon flights usually terminated well before sunset, although in the forest light had begun to fade. Although the nest entrance was examined after dark in the evening and before sunrise in the morning it was never closed, although *Euglossa cordata* (Linn.) and *E. variabilis* Friese usually close the entrances to their nests at night (Bennett, 1966).

(b) Observations on *Exaerete*: During the days that the nest was under close observation one *Exaerete* adult was frequently observed resting on foliage one to three meters from the nest entrance. On one day two adults were present. On three separate occasions a *Eulaema* female, returning when an *Exaerete* was flying near the entrance, attempted to drive it away and failing to do so flew away thereafter. Observed entries into the nest are noted in

TABLE 1. Summary of flight activity of *Eulaema terminata* and *Exaerete* sp., April 1964

Date	15	16	21	22	23	24	25
<i>Eulaema</i>							
A.M.							
(1) 1st ♀ departed	n.r.	5:30	n.r.	5:45	5:40	5:45	6:05
1st ♀ returned	5:51	5:55	n.r.	5:55	6:02	6:01	7:10
(3) Activity terminated	10:10	11:10	11:35	11:34	11:26	11:21	11:31
(4) Total no. of trips**	(12)15	(19)20	n.r.	(15)15	(9)9	(6)6	(10)11
P.M.							
(5) 1st ♀ departed	2:21	3:15	3:05	3:10	3:11	4:09	3:12
(6) 1st ♀ returned	4:20	3:31	3:30	3:26	3:41	4:23	3:41
(7) Flight activity terminated	5:33	6:18	5:21	5:56	6:04	6:49	5:55
(8) Total no. of trips**	(5)5	(8)8	(9)7	(7)8	(11)9	(6)5	(6)8
<i>Exaerete</i>							
(9) Entered nest	8:45	—	7:01	6:30*	6:25	6:10*	11:02
(10) Left nest	8:47	—	7:02		6:26		11:44

* Approached but did not enter.

** Recorded departures and arrivals of all bees (figures in brackets are departures; unbracketed are return trips).

n.r. Not recorded.

Table 1. It seems unlikely in view of observations reported below that oviposition could have occurred except on the final visit when the *Exaerete* female remained in the nest for 45 minutes. Unfortunately the specific identity of the *Exaerete* females was not determined.

Observations were suspended while I was absent from Trinidad and I was not able to visit the site again until September 3. During this period the top of the tree was snapped off when a larger neighboring tree was uprooted during a tropical storm. When the standing trunk of the tree was felled the center proved to be rotten with a somewhat irregular cavity, ca. 8 cm. in diameter, extending 20 cm. below the nest opening and upward about 40 cm. The group of cells that had been attached to the side of the trunk about 2 m. from ground level, i.e., above the entrance hole, had become dislodged and the cell mass broken into several pieces. These, although partially reconstructed (fig. 1), were not in a suitable condition for analysis. Bees had apparently emerged from some, whereas smaller irregular holes in others suggested that predation by ants may have occurred. One cell contained the cocoon of a Mutillid wasp, apparently the first record of the family from a species of *Eulaema*, although Dodson (1966) records an unidentified species from *Euglossa* spp.

ASSOCIATION WITH *Euplusia surinamensis*

Adults of *Exaerete dentata* have been reared from cells of *Euplusia surinamensis* obtained from diverse nesting sites on a number of occasions. As most of these nesting sites were located in crevices between stacked lumber or in



FIG. 1. Cells of *Eulaema terminata* removed from nest in hollow tree.

cracks between joists and floor boards beneath houses elevated on pillars, the activities of neither of the bees could be readily observed. Similarly, the occasional cells of *Euplusia* found in abandoned galleries of *Xylocopa frontalis* or in the *Euglossa* nesting boxes described briefly by Bennett (1965) have never been encountered when provisioning was under way.

The discovery that *Euplusia surinamensis* frequently nests in crevices in eroded shale sea cliffs near Balandra offered an opportunity to make limited observations on its parasite, *Exaerete dentata*.

(a) Description of the *Euplusia* nesting site: Owing to the gradual encroachment of the sea, sections of the shale comprising the seacliffs periodically topple into the sea as the bases of the cliffs are undermined. When this occurs a series of crevices 1 cm. or more in depth and frequently 15 to 20 cm. in width and length is formed. These crevices are at varying slopes, depending on the angle at which the rock strata came to rest after the last major geological upheaval. The crevices most frequently occupied are those sloping upward into the cliff. Crevices on relatively open, exposed cliffs are exploited as nesting sites less frequently than those in sheltered bays or those in small caves.

The cave where observations were made was quite small, the entrance ca. 1.3 m. high and 1.8 m. wide opening into a small chamber about 1.8 m. high,

2 m. wide, and 2 m. deep. At high tide the waves break against the cliff and the resulting spray frequently moistens the cells. However, adults of both *Euplusia surinamensis* and *Exaerete dentata* have been frequently reared from badly weathered groups of cells taken from this cave.

As the cells of *Euplusia* spp., including those of *E. surinamensis* (Dodson, 1966; Zucchi et al., 1969) and of *E. violaceae* (Blanchard; Sakagami and Michener, 1965) have been described, they will not be redescribed in detail. Constructed of resin and pieces of bark in linear series, each cell after it is formed is provisioned, and after an egg is deposited, sealed with smaller pieces of bark held together by resin.

(b) Notes on *Exaerete*: At 9:05 A.M. on May 2, 1966, when observations were commenced, a female of *E. dentata* was already examining a recently sealed cell. Although apparently quite nervous initially (evidenced by the rapid alternate telescoping and expansion of the abdomen), she examined the slightly concave end of the cell with both antennae and mandibles and began to remove bits of bark from the cell cap. Although some bits of the bark fell to the ground, most were attached by the female to the inside of the partially formed cell next in sequence. By 9:19 A.M. the cell cap was opened sufficiently to permit insertion of the head and part of the thorax into the cell. On one occasion during this period of opening the cell the female lost her footing and fell almost to the floor of the cave before taking wing and returning to the cell. At 9:20 the bee removed the egg of *Euplusia* which had previously reposed on the surface of the cell provisions and crushed it with her mandibles. Following a short period of activity during which the head remained within the cell, possibly rearranging the provisions slightly, the female reversed her position and inserted the tip of the abdomen into the cell (9:22). She remained motionless for several seconds; then, extending the tip of the abdomen slightly further, deposited an egg (9:24). She then commenced the resealing of the cell, utilizing the bits of chewed wood and resin removed a few minutes earlier. At 9:40 the female "lost her footing," dropped from the cell, and flew away. She returned at 9:42 and after several seconds' search relocated the cell, alighted, and continued her activities. When she alighted the female had a bit of chewed wood in her mandibles; this was probably present when she dropped from the cell. When the cell was almost sealed the bee again "fell off" at 10:05, flew about the face of the cliff, approached a partially provisioned *Euplusia* cell about 3 meters from the one she had been sealing, but did not alight. Returning to the original cell a few seconds later, she spent another ten minutes packing and smoothing the cell cap before again falling from the cell and alighting on my shirt where she rested for almost a minute. She still had bits of chewed wood and resin between her mandibles. Leaving my shirt she flew out of the cave, hovered

in front of the partially provisioned cell visited earlier, alighted, explored the cell contents, and deposited the chewed wood at the cell entrance. She stayed in the cell for almost one minute, flew off, and entered another crevice quite close to the cell which had been recently sealed and where a *Euplusia* female had entered with bits of bark earlier in the morning. She spent only a few seconds before again taking flight. After flying in an exploratory fashion about the face of the cliff, the bee flew around the point into the next small bay and after moving back and forth along the face of the cliff flew upward over the cliff and disappeared.

Somewhat similar although less detailed observations were made at another site in company with E. Kjellesvig-Waering on August 2, 1966, at a small seaside hotel at Mayaro, Trinidad. Three *Exaerete* females were observed near a nesting site of *E. surinamensis* where several individuals were nesting in hollow clay tiles at the top of the end wall of the porch. One end of the tiles was open, the other embedded in the wall of the building. Although there were numerous cells, the adults of *Euplusia* and *Exaerete* could be observed only indistinctly from a distance of 1.5 m. because a concrete beam projecting downward only few centimeters from the open end of the tiles prevented closer scrutiny. Over a two-hour period one female of *E. dentata* remained stationary at the entrance of a cell; she appeared to be resting and her behavior was quite unlike that of the female observed at the Balandra site. Two females collected at this site, as well as several adults that emerged from the Balandra site, were determined as *E. dentata*.

DISCUSSION

Although a female of an unidentified species of *Exaerete* was observed to enter the nesting site of *Eulaema terminata* on several occasions, there was no indication that she was readily accepted or lived in harmony with the females of *E. terminata*. Similarly, observations on *Exaerete dentata* parasitic on *Euplusia surinamensis* indicate that the habits of members of the genus are more like those of parasites of solitary bees than to those of *Psithyrus* (discussed by Bohart, 1970).

It is of interest to note that the habit of opening a recently completed host cell, removing the host's egg, and then after depositing its own egg resealing the cell is very similar to that reported for *Stelis (Odontostelis) bilineolata* (Spinola), the only other bee parasitic on a Euglossine for which details of the biology are known (Bennett, 1966). Unlike *S. binotata*, which is unrelated to its hosts, *Euglossa cordata* and *E. variabilis* Friese, and drives the host bee permanently from the nest, the attack by *Exaerete dentata*, as determined subsequently by the emergence pattern from series of cells, does not deter the *Euplusia* female from constructing additional cells in the same series on top of one opened and resealed by *Exaerete*.

The only other parasitic bees whose females open host cells, presumably destroy the host egg, and then presumably reseal the cells are the Halictid parasites such as *Sphecodes*. Details of behavior have not been observed, but closed cells containing no host egg or young are well known. In some cases the host (or hosts) is killed or leaves the nest, while in others they remain (see Bohart, 1970).

Acknowledgments: I am indebted to my field collector Mr. D. Bharath, who located the nest of *Eulaema terminata* and at great personal discomfort spent several days and nights in the Nariva Swamp carrying out many of the observations reported for this species. The *Euplusia* nesting site at Balandra was the joint discovery of my wife Betty and my son Philip. Dr. J. G. Rozen and J. S. Moure, CMF identified the specimens of *Exaerete* and reported the occurrence of three species of the genus in Trinidad.

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